HIGHER CLASSIFICATION OF THE BURROWING MAYFLIES (EPHEMEROPTERA: SCAPPHODONTA)[1]

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ABSTRACT: A revised cladogram of the monophyletic groups of genera constituting the tusked burrowing mayflies (infraorder Scapphodonta) is presented, based in part on new analyses of relationships that have recently appeared in the literature. A new strict phylogenetic higher classification of Scapphodonta that incorporates both extant and extinct taxa and that reflects the revised cladogram is presented. Aspects include the new superfamilies Potamanthoidea (Potamanthidae and Australiphemeridae) and Euthyplocioidea (Euthyplociidae and Pristiplociidae), and a newly restricted Ephemeroidea (Ichthybotidae, Ephemeridae s.s., Palingeniidae and Polymitarcyidae s.s.). Sequencing conventions allow recognition of multiple scapphodont superfamilies, ephemeroid families and polymitarcyid subfamilies. *Pentagenia* is placed in Palingeniidae, and *Cretomitarcys* is removed from the Scapphodonta.

KEY WORDS: Higher classification, burrowing mayflies, Ephemeroptera, Scapphodonta

The Ephemeroptera infraorder Scapphodonta is equivalent to what was recently considered the superfamily Ephemeroidea by McCafferty (1991) and others. It is a grouping hypothesized to be the sister clade of the infraorder Pannota, or the pannote mayflies, within the suborder Furcatergalia (McCafferty and Wang 2000). The Scapphodonta are technically the "tusked burrowing mayflies" and as a monophyletic group demonstrate a defining apomorphy of having larval tusks derived from the outer body of the mandible (e.g., see Bae and McCafferty 1995). Scapphodonta does not include other furcatergalian mayflies constituting the Behningiidae (the infraorder Palpotarsa, or tuskless "primitive burrowing mayflies") or the few specialized Leptophlebiidae (infraorder Lanceolata) that are also known to burrow and may possess tusks that are not homologous with scapphodont tusks (e.g., see Bae and McCafferty 1995, Edmunds and McCafferty 1996).

McCafferty (1991) presented hypothetical relationships of burrowing mayfly groups that served as a basis for exemplifying the application of strict phylogenetic schemes of higher classification to Ephemeroptera. This resulted in a conservative familial classification of the Ephemeroidea, or Scapphodonta, that has to a large degree been followed throughout the world in recent years. That classification consisted of only four families: Australiphemeridae, Potamanthidae, Ephemeridae, and Polymitarcyidae. Ephemeridae was divided into subfamilies Ichthybotinae, Ephemerinae, Hexageniinae, Pentageniinae and Palingeniinae. All of these subfamilies except Hexageniinae had been recognized as families at some point prior to 1991. Ichthybotinae, which had originally been considered a family by Demoulin (1957a) but historically not such by others, was reestablished by McCafferty (1999). Polymitarcyidae was divided into the subfamilies Pristiplociinae, Euthyplociinae, Exeuthyplociinae, Asthenopodinae, Campsurinae and Polymitarcyinae.

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Previous to this, however, the latter three had been considered in a more restricted family Polymitarcyidae, and Euthyplociinae and Exeuthyplociinae had been considered in the family Euthyplociidae. Pristiplociidae was given familial status by McCafferty (1997).

Since the McCafferty (1991) study, certain characters from internal anatomy that had been documented by Landa and Soldán (1985) and used by McCafferty (1991) have proven to be unreliable mainly because they had been based on too few exemplars within taxa. In addition, important new phylogenetic analyses of burrowing mayflies were made by Bae and McCafferty (1995) and Kluge (2003). These findings along with ancillary studies by McCafferty (1999) and McCafferty and Wang (2000) have prompted a reevaluation and reclassification of the Scapphodonta as presented below.

PHYLOGENY

Compared to the analysis of McCafferty (1991), the phylogenetic analysis based on tusk morphology given by Bae and McCafferty (1995) offered a more convincing hypothesis of branching sequences of certain clades, one example being that the *Campsurus* group (Campsurinae) and *Asthenopus* group (Asthenopodinae) were sister clades rather than the *Campsurus* group and the *Ephoron* group (Polymitarcyinae). The *Campsurus* group and *Asthenopus* group tusks were shown to share an apomorphic large mediobasal spine, medioapical crenulation and ventral setation. The Bae and McCafferty (1995) study also showed that within the extant Scapphodonta excluding the basally derived *Potamanthus* group (Potamanthidae), the *Euthyplocia* + *Exeuthyplocia* groups (Euthyplociinae and Exeuthyplociinae) do not share additional apomorphies with other clades, but have tusks with unique medial and lateral rows of setae. Among remaining clades, the *Pentagenia* group (Pentageniinae) + the *Palingenia* group (Palingeniinae) were hypothesized to be derived from an ancestor common with the *Ephemera* group (Ephemerinae) + *Hexagenia* group (Hexageniinae) rather than from within the *Hexagenia* group. This is supported by the apomorphic strong basal arch of the tusks in *Ephemera* + *Hexagenia* groups but not *Pentagenia* + *Palingenia* groups, and by the apomorphic U-shaped or arched arrangement of setae basally on the tusks found in *Pentagenia* + *Palingenia* groups but not the *Ephemera* + *Hexagenia* groups.

Kluge (2003) also presented data that suggested the *Euthyplocia* + *Exeuthyplocia* groups to have a basal branching position among non-potamanthid Scapphodonta, and gave another synapomorphy for these groups, i.e., the unique anteriorly developed clypeus. In addition, he hypothesized a sister relationship between a clade consisting of the *Ephoron* + *Campsurus* + *Asthenopus* groups and a clade consisting of the *Pentagenia* + *Palingenia* groups. For example, these clades were shown to share apomorphies including forecoxae that are nearly contiguous, and an inner basal convexity of the larval forefemora with a curved arrangement of setae [Kluge also included use of the arrangement of setae at the base of the tusk that had been introduced by Bae and McCafferty (1995) for the *Pentagenia* + *Palingenia* groups, see above]. Although Kluge (2003) stated that two-segmented maxillary and labial palps represented another synapomorphy for the *Pentagenia* + *Palingenia* + *Ephoron* + *Campsurus* + *Asthenopus* groups, the assigned character states of two- or three-segmented palps are not consistently distributed within this latter grouping or its hypothesized sister clade, or nearest outgroup (*Ephemera* + *Hexagenia* groups). For example, larvae of *Pentagenia vittigera* (Walsh) frequently have a second segmentation line in the maxillary palps, and the labial palps of genera of the *Hexagenia* group (e.g., *Litobrancha* McCafferty and some *Hexagenia* Walsh) are commonly two-segmented, as are species within the *Ephemera* group (e.g., at least some *Afromera* Demoulin). Kluge's statement of synapomorphy might better have been limited to the thicker, clublike, rounded palps (versus narrow, falcate or truncate palps).

The hypothesis of the sister relationship of *Pentagenia* + *Palingenia* groups and the *Ephoron* + *Campsurus* + *Asthenopus* groups is considerably different from the proposed relationships of Palingeniidae and Ephemeridae first given by McCafferty (1972) and McCafferty and Edmunds (1976) and expressed in the McCafferty (1991) scheme. However, behavioral evolutionary trends among the Scapphodonta that were theorized by Bae and McCafferty (1995) remain for the most part compatible with Kluge's phylogenetic hypothesis. In addition, functional and behavioral differences associated with burrowing in *Hexagenia* and *Pentagenia* Walsh (Keltner and McCafferty 1986) as well as similarities between *Pentagenia* and *Tortopus* Needham and Murphy (*Campsurus* group) (McCafferty unpublished) are also compatible with Kluge's hypothesis. Essentially, *Pentagenia* + *Palingenia* + *Ephoron* + *Campsurus* + *Asthenopus* groups demonstrate what appears to be well-armored and heavily sclerotized heads and tusks associated with an advanced type of burrowing that can involve chiseling into hard substrates or compacted substrates such as clay (e.g., Edmunds et al. 1956, Scott et al. 1959, Keltner and McCafferty 1986, Bae and McCafferty 1995, Edmunds and McCafferty 1996). Although the capacity for this type of burrowing may not be strictly realized in the individual microhabitats of every species within the clade, it does not exist in other Scapphodonta. The significant change from the Bae and McCafferty (1995) interpretation is that this behavioral trend evolved only once rather than twice independently within the Scapphodonta.

Kluge's (2003) additional hypothesis of a derivation of Behningiidae within the Scapphodonta is not convincing because it was based on suppositions that numerous characters only possibly derived in common with the Scapphodonta were lost subsequently in Behningiidae. Behningiidae forewings are unlike Scapphodonta in general and the most plesiotypic adults of Pannota (Neoephemeridae) in that they demonstrate only an inconsistent, slight tendency for basal vein curvature (possibly but not necessarily suggesting a phylogenetic branch basad of the common ancestor of the Scapphodonta and Pannota); larvae do not possess tusks or other apomorphic structures that are associated with burrowing in Scapphodonta (and there is no evidence that precursors to Behningiidae possessed tusks or such structures); and larvae are known to be an unusual type of interstitial sand-dwellers with predatory habits (Keffermüller 1959, Tshernova and Bajkova 1960, McCafferty 1975, Tsui and Hubbard 1979), a biology fundamentally dissimilar to that found among the Scapphodonta. In addition, the considerable unique morphology associated with both the larvae (e.g., legs) and adults (e.g., genitalia) of Behningiidae (see McCafferty 1979, Peters and Gillies 1991) does not appear to be derived in common with, or derived from, any Scapphodonta.

Considering all of the above, certain phylogenetic modifications can now be made to the cladogram of Scapphodonta originally offered by McCafferty (1991). Such a revised cladogram of the monophyletic groups of genera of the Scapphodonta is shown in Figure 1.

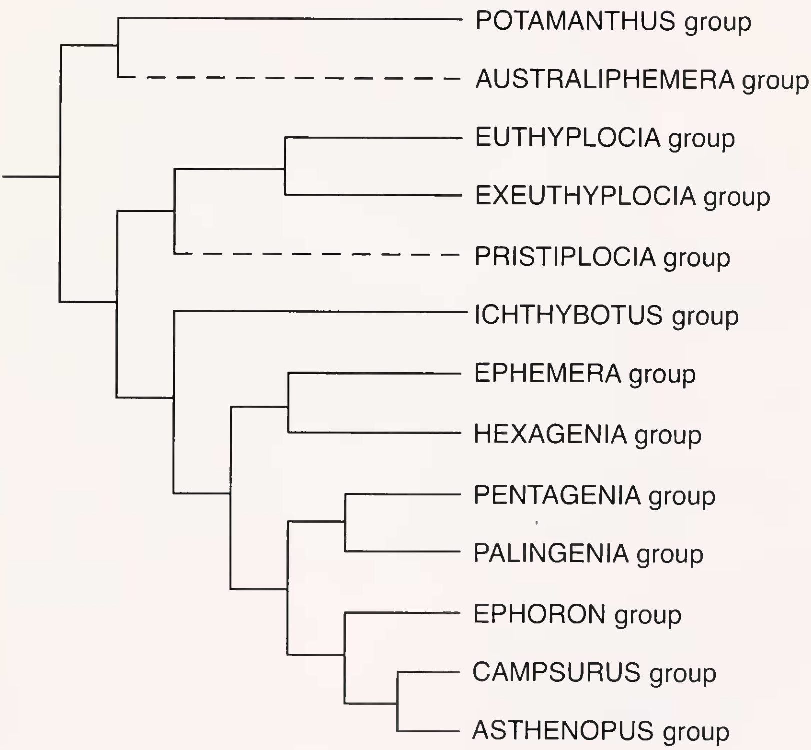

Fig. 1. Hypothesized cladogram of monophyletic groups of genera of Scapphodonta. See text for defining apomorphies.

CLASSIFICATION

The new phylogeny in turn requires a new, strict phylogenetic higher classification designed within the constructs of Linnaean hierarchy. Such a classification (Table 1) can reflect the branching sequences of major clades (Fig. 1) without the use of any numerical coding system.

Table 1. Higher classification of the Scapphodonta. Within superfamilies, single asterisked taxa are known from fossils only, and double asterisked taxa include both extant and extinct species. Bracketed genera are those whose relationships within the monophyletic group of genera remain unresolved. General distributions are given parenthetically.

Superfamily Potamanthoidea, n. superfam.
  Family Potamanthidae Albarda (Holarctic, Oriental)
      Genus *Rhoenanthus* Eaton
        Subgenus *Rhoenanthus* s.s.
        Subgenus *Potamanthindus* Lestage
      Genus *Anthopotamus* McCafferty & Bae
      Genus *Potamanthus* Pictet
        Subgenus *Potamanthus* s.s.
        Subgenus *Stygifloris* Bae, McCafferty & Edmunds
  Family Australiphemeridae* McCafferty (Pangaean)
    [Genera *Australiphemera* McCafferty, *Borephemera* Sinitshenkova, *Microphemera* McCafferty, *Paleoanthus* Kluge]

Superfamily Euthyplocioidea, n. superfam.
  Family Euthyplociidae Lestage (Pantropical)
    Subfamily Euthyplociinae s.s. (Pantropical)
      [Genera *Campylocia* Needham & Murphy, *Euthyplocia* Eaton, *Mesoplocia* Demoulin, *Polyplocia* Lestage, *Proboscidoplocia* Demoulin]
    Subfamily Exeuthyplociinae Gillies (Afrotropical)
      Genus *Afroplocia* Lestage
      Genus *Exeuthyplocia* Lestage
  Family Pristiplociidae* McCafferty (Gondwanan)
      Genus *Pristiplocia* McCafferty

Superfamily Ephemeroidea
  Family Ichthybotidae Demoulin (New Zealand)
      Genus *Ichthybotus* Eaton
  Family Ephemeridae** Latreille (nec Australian)
    Subfamily Ephemerinae** s.s. (nec Neotropical, nec Australian)
      Genus *Ephemera*** Linnaeus
        Subgenus *Ephemera* s.s.
        Subgenus *Aethephemera* McCafferty & Edmunds
      Genus *Afromera* Demoulin
    Subfamily Hexageniinae** McCafferty (nec Australian)
      Genus *Denina** McCafferty
      Genus *Hexagenia*** Walsh
        Subgenus *Hexagenia*** s.s.
        Subgenus *Pseudeatonica* Spieth

Genus *Litobrancha*** McCafferty
Genus *Eatonigenia* Ulmer
Genus *Eatonica* Navás
Family Palingeniidae Albarda (nec Australian, nec Neotropical)
Subfamily Pentageniinae McCafferty (Nearctic)
Genus *Pentagenia* Walsh
Subfamily Palingeniinae s.s. (E. Hemisphere, nec Australian)
[Genera *Anagenesia* Eaton, *Chankagenesia* Buldovsky, *Cheirogenesia* Demoulin, *Mortogenesia* Lestage, *Palingenia* Burmeister, *Plethogenesia* Ulmer]
Family Polymitarcyidae** Banks (nec Australian)
Subfamily Polymitarcyinae s.s. (nec Australian, nec Neotropical)
Genus *Ephoron* Williamson
Subfamily Campsurinae** Traver (Neotropical, Nearctic)
Genus *Campsurus* Eaton
Genus *Tortopus* Needham & Murphy
[Genus *Mesopalingea** Whalley & Jarzembowski (Laurasian)]
Subfamily Asthenopodinae Edmunds and Traver (Pantropical)
Genus *Asthenopus* Eaton
Genus *Povilla* Eaton
[Genus *Asthenopodichnium** Thenius]

Sequencing conventions (see Wiley 1981) are utilized for recognizing three superfamilies within Scapphodonta, four families within the Ephemeroidea, and three subfamilies within the Polymitarcyidae. The hypothesized cladogram of superfamilies, families and subfamilies can be reproduced precisely from their linear hierarchical classification. Within certain families or subfamilies, the phylogeny of genera has been hypothesized previously. For the basis of the linear sequence of taxa within Potamanthidae, see Bae and McCafferty (1991); and for the basis of the linear sequence of taxa within the Ephemeridae, see McCafferty (1973, 1987), McCafferty and Gillies (1979) and McCafferty and Sinitshenkova (1983). Those genera that are listed alphabetically within brackets in Table 1 require cladistic analysis before their interrelationships can be hypothesized.

The placement of the extinct families Australiphemeridae and Pristiplociidae (shown by dashed lines in Fig. 1) is presently hypothesized from morphological data limited to alate fossils. Some recent genera in other families of Scapphodonta are represented in the Cenozoic, but no recent genera are represented in the fossil record previous to the Cenozoic. The present and historical placement of Mesozoic genera among recent families is either unfounded or provisionally based on limited morphological data. *Mesogenesia* Tshernova was originally described in the Palingeniidae (Tshernova 1977), and Demoulin (1957b) considered *Parabaetis* Haupt in Ephemeridae, but both genera were shown not to belong to the Scapphodonta by McCafferty (1990). The genus *Mesopalingea* Whalley and Jarzembowski (1985) was originally placed in the family Palingeniidae. However, based on the morphology of the well-fossilized larval tusks, the genus should provisionally be placed in the subfamily Campsurinae of the family Polymitarcyidae. This would represent a rare instance of a Mesozoic family of Scapphodonta surviving the K-T boundary and the mass extinctions associated with that critical juncture. *Cretomitarcys* Sinitshenkova (subfamily Cretomitarcyinae Sinitshenkova) was based on an alate specimen found in upper Cretaceous New Jersey amber. Sinitshenkova's (2000) placement of this mayfly in the family Polymitarcyidae is not supportable because wing venation characteristics, including lack of fundamental basal vein curvature and the orientation of cubital and anal veins in the forewings are not those of Scapphodonta. Instead, forewing venation, such as the uninterrupted extension of veins CuP and A1 from the base of the forewing to the outer margin, suggests an extinct family (Cretomitarcyidae, n. stat.) of the suborder Carapacea, and extensive longitudinal venation of the hindwing may further suggest a relationship with the family Baetiscidae [compare Figs. 3 and 4 of Sinitshenkova (2000) with Figs. 226a and b of Edmunds et al. (1976)].

An important aspect of the new classification of Scapphodonta taxa is the recognition of two additional superfamilies and the restriction of the concept of the superfamily Ephemeroidea. The placement of the North American genus *Pentagenia* is also of some significance because it adds another family of mayflies (Palingeniidae) to the North American fauna. The placement of *Pentagenia* as such had been proposed by McCafferty and Edmunds (1976), but at that time it was supposed that the Palingeniidae had arisen from within Ephemeridae, and thus recognition of the two families was later deemed incompatible with a phylogenetic classification because of assumed paraphyly (McCafferty 1991). The family Ichthybotidae is somewhat an anomaly because of its geographic restriction to New Zealand in the absence of any other known Amphinotic Scapphodonta. McCafferty (1999) explained it as being relictual, suggesting that Scapphodonta was probably more widely distributed in the Southern Hemisphere prior to the K-T extinctions.

The familial classification presented here, including the linear sequence of families, is for the most part similar to that given a half century ago by Edmunds and Traver (1954). This may seem remarkable if one considers that the former classification was phenetic based. Some families have been slightly redefined or restricted in the new classification, Behningiidae has been removed; and the familial classification, including extinct families, would not be allowable under strict rules of phylogenetic classification within a single superfamily. Nevertheless, the comparison illustrates that family recognition in mayflies based on phenetic analyses may to a large degree be congruent with family recognition within a strict phylogenetic system. This should not detract from the importance of continuing to test and refine classifications based on cladistics, but instead illustrates that relative stability can sometimes be maintained by choosing among strict phylogenetic classification options.

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